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Review article

Banded together: a review of the factors favouring group living in a social carnivore, the banded mongoose *Mungos mungo* (Carnivora: Herpestidae)

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As most species of the order Carnivora are solitary (Gittleman 1989), there is ongoing debate over the evolution and maintenance of sociality in carnivores. It has been hypothesised that five factors reduce the costs and/or increase the benefits of tolerating conspecifics (Creel and Macdonald 1995): (1) high abundance and renewability of prey; (2) constraints on dispersal and benefits of philopatry; (3) improved acquisition and defence of resources; (4) enhanced anti-predatory defence; and (5) alloparental care.

Mainly because of differences in feeding ecology, it has been speculated that selective forces behind the evolution and maintenance of sociality in mongooses (Herpestidae) may differ from those in carnivores in general (Rood 1975, 1986, Gorman 1979, Waser 1981, Waser and Waser 1985). Characteristically, most social mongooses are insectivorous, small and diurnal and live in open habitats (Gorman 1979, Rood 1986), which is in accordance with a recent analysis of genetic and behavioural data on the origin of sociality in mongooses (Veron et al. 2004).

Here, to shed further light on the factors favouring group living in carnivores, the five hypotheses outlined above are reviewed in relation to one such insectivorous, small, diurnal social mongoose living in open habitats, the banded mongoose *Mungos mungo* (Gmelin 1788).

Hypothesis 1: high abundance and renewability of prey When foraging, banded mongooses scatter and mainly feed on insects and other invertebrates, supplementing their diet with small vertebrates (Neal 1970, Rood 1975, 1982, Hiscocks and Perrin 1991). Both the abundance and renewal rate of their main prey are high (Waser 1981). High abundance and renewability of insects, together with relatively low competition in catching them, were probably a precondition for the evolution of group living in mongooses (Rood 1975, 1986, Gorman 1979, Waser 1981, Waser and Waser 1985).

Hypothesis 2: constraints on dispersal and benefits of philopatry Dispersal involves substantial costs in banded mongooses (Cant et al. 2001), thus posing considerable constraints on leaving the natal pack. In line with this, banded mongooses exhibit low variance in within-group relatedness (Waldick et al. 2003), with no apparent avoidance or negative consequences of inbreeding (Gilchrist et al. 2004, Gilchrist 2006a). Despite a loose linear dominance hierarchy (without apparent effects on a variety of demographic and social variables) within a pack, there is no evidence of effective pre- or post-parturition reproductive suppression of subordinates in either sex (Cant 2000, De Luca and Ginsberg 2001, Gilchrist et al. 2004). As a result, there is a good chance for philopatric banded mongooses to reproduce in their natal pack.

Hypothesis 3: improved acquisition and defence of resources Banded mongooses cooperatively attack prey, take prey away from other predators and vocally attract other pack members to rich food patches (Simpson 1964, Rood 1975, Messeri et al. 1987). Aggressive territorial conflicts between banded mongoose packs are common, particularly during oestrus periods, with larger packs dominating smaller ones (Rood 1975, 1986, Cant et al. 2002, Gilchrist and Otali 2002, Müller and Manser 2007). Individuals in larger packs might be more likely to engage in extra-group copulations observed during such encounters (Rood 1975, Cant et al. 2002, Gilchrist et al. 2004).

Hypothesis 4: enhanced anti-predatory defence Banded mongooses cooperatively harass and even kill predators, bunch together around pups when disturbed in the open, and rescue other pack members from predators (Simpson 1964, Neal 1970, Rood 1975, 1982, 1983, 1986). Furthermore, members guard the pack through vigilance, emit alarm calls when danger threatens, and rush to help individuals calling in distress (Neal 1970, Rood 1975, Messeri et al. 1987). Group living in mongooses probably evolved as an anti-predatory response by small, diurnal animals living in open habitats (Rood 1975, 1986, Gorman 1979).

Hypothesis 5: alloparental care Within a banded mongoose pack, several females come into oestrus and subsequently produce their litters synchronously (Neal 1970, Rood 1974, 1975, 1986, Waser et al. 1995, Cant 2000, Gilchrist et al. 2004, Gilchrist 2006a,b). Lactating females apparently nurse any of the pups without discrimination and pack members cooperate in raising the pups around the communal den (Neal 1970, Rood 1974, 1975, 1982, 1986, Viljoen 1980, Waser et al. 1995, Cant 2003). Once the pups start to accompany the adults on their daily foraging trips, pack members "escort" and help provision the pups in a remarkably stable associa-

tion (Gilchrist 2004, Hodge 2005, Bell 2007, Gilchrist and Russell 2007).

Banded mongooses are a rare example of an egalitarian mammalian society, in that they both lack a distinct dominance hierarchy and have an apparently low reproductive skew. As a consequence of egalitarianism, an individual's chance of successful reproduction on reaching adulthood is good in its natal pack, especially as there is no apparent avoidance and negative consequence of inbreeding (Gilchrist et al. 2004, Gilchrist 2006a). Egalitarianism might thus be regarded as an incentive to stay that, similar to high abundance and renewability of prey, reduces an individual's costs of tolerating conspecifics and at the same time allows it to enjoy the equitably distributed benefits of living in a group (i.e., improved acquisition and defence of resources, enhanced anti-predatory defence, and alloparental care).

Therefore, increased (immediate and often mutualistic) direct and indirect fitness benefits accruing to non-dispersers (resulting from low variance in within-group relatedness; Waldick et al. 2003), together with considerable constraints on dispersal (Cant et al. 2001), are likely to be an additional factor favouring group living in banded mongooses as a plural breeder with communal care. Among social carnivores (Packer et al. 2001), the rare combination of plural breeding and low reproductive skew is more prevalent in species with relatively low costs of reproduction, which holds true for banded mongooses (Gittleman 1989, Creel and Creel 1991, Creel and Macdonald 1995).

In conclusion, it is remarkable that all factors proposed to reduce the costs and/or increase the benefits of tolerating conspecifics, and thus to favour group living, in carnivores (Creel and Macdonald 1995) are found to act in concert on a single species, the banded mongoose.

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